THE MYOLOGY OF *SCELOPORUS C. CLARKI* BAIRD AND GIRARD (REPTILIA: IGUANIDAE)

by

D. M. Secoy[1]

ABSTRACT

Examination of the complete musculature of *Sceloporus clarki clarki* Baird and Girard and seven other species of *Sceloporus* revealed variation among species of *Sceloporus* and between *Sceloporus* and other iguanid lizards. The muscles in which the greatest variation was found were the intermandibularis group, the constrictor colli, the episterno-cleido-mastoideus, the episternohyoideus, the coracoid head of the triceps, the costocoracoid and the flexor tibialis externus. This study indicates: (1) *Sceloporus* is more closely allied to *Crotaphytus* than to the ground-dwelling iguanines;(2) the possibility of the basal stock of *Sceloporus* being arboreal, and, (3) *Sceloporus* is a genus in the process of rapid differentiation.

INTRODUCTION

Even a cursory glance at the literature dealing with the morphology of the suborder Lacertilia reveals the scarcity and scattered nature of studies concerned with the soft anatomy.

The myology of the entire body has been described in varying detail in eight genera of the suborder Lacertilia: *Iguana* (Mivart, 1867), *Chamaeleon* (Mivart, 1870),*Platydactylus* (Sanders, 1870), *Liolepis* (Sanders, 1872), *Phrynosoma* (Sanders, 1874), *Pseudopus* (Humphry, 1872), *Chlamydosaurus* (de Vis, 1883), and *Uromastix* (George, 1948) have been examined and described. Laboratory dissection guides showing the antomy of *Crotaphytus* (Davis, 1934) and *Agama* (Harris, 1963) are brief.

A search of the literature for descriptions of portions of the anatomy of a genus, or comparative works examining representatives of different genera or families is much more rewarding. The former includes the recent work by Oelrich (1956) on the head of *Ctenosaura pectinata*, Avery and Tanner's paper (1964) on the head and thorax of *Sauromalus*, Robison and Tanner's paper (1962) on the anterior region of *Crotaphytus* and *Gambelia*, and Jenkins and Tanner's paper (1968) on *Phrynosoma*.

Comparative studies have been divided into three main groups: those concerned with the muscles of the jaw articulation; those which have examined the variation in the muscles connected with the hyoid apparatus; and those head of reptiles, as is the case with other vertebrate groups, has been studied most extensively. The works on the jaw muscles include those of Versluys (1904), Bradley (1903), Adams (1919), Lakjer (1926), and Haas (1960). Some of the more important works on the hyoid apparatus are those by Zavattari (1908), Gandolfi (1908), and Gnanamuthu (1936). Edgeworth's treatise (1935) on cranial muscles includes all head musculature and discusses the homologies of structures extensively, although Brock (1938) disagrees with his ideas of muscle origins. Camp (1923) has used the numerous generic descriptions of the hyoid and its associated musculature in the construction of his lizard classification.

The other area of intensive interest and work has been in limb musculature. Romer (1922, 1923, 1942) has established homologies in the pelvic limb muscles among the several reptilian groups based on his research and that of Gadow (1882). Haines (1934, 1935) and Appleton (1928) have also discussed the homologies of the pelvic and thigh muscles. The anterior limb and pectoral girdle have been studied by Fürbringer (1876), Romer (1924, 1944), McMurrich (1903, 1903a), and Howell (1938).

Since its description by Wiegmann in 1828 *Sceloporus* has been one of the most intensively studied of the New World iguanid lizards. The

[1]Department of Biology, University of Saskatchewan, Regina, Saskatchewan, Canada.

large size of the genus and its broad distribution concerned with the muscles of the limbs. The have made it ideal for studies on taxonomy and distribution. The same two factors have made it unwieldy and a deterrent to those who wish to study the entire genus.

Early studies of the genus include those of Dumeril and Bibron (1837), Boulenger (1897), and Cope (1900). The definitive work on the genus is that of Hobart Smith (1936, 1937, 1937a, 1938, 1939). These studies have been based on external characteristics and the only mention of skeletal or soft anatomy is at the generic level.

The osteology of the genus has been described piecemeal, usually in conjunction with that of other reptiles. Cope (1892) gives a complete description of the skull and skeleton but gives no figures. Camp (1923), in his work on lizard classification, refers to *Sceloporus* in the discussion of many of the skeletal characters. Stokely (1950) mentions the possibility of the occurrence of an intermedium in *Sceloporus*. Hotton (1955) discusses the dentition of *Sceloporus graciosus*, *S. magister* and *S. undulatus* in relation to their prey choice. Romer (1956) illustrates various skeletal elements in his treatise on reptilian osteology. Lundelius (1957) made a statistical analysis of the skeletal adaptations of *Sceloporus olivaceus* and *S. undulatus hyacinthinus* in relation to their environments. Jollie (1960) included *Sceloporus undulatus* in his analysis of the lizard skull. Avery and Tanner (1964) illustrated and discussed the variation in the wrist bones of several genera of iguanids, including *Sceloporus*. Etheridge (1964, 1965, 1967) discussed and illustrated several skeletal elements of *Sceloporus* in his studies of skeletal variation within the Iguanidae. Miller (1966) discussed *Sceloporus* in his work on the cochlear duct in the Lacertilia.

The myology has been less well studied. Camp (1923) mentions the genus in his discussion of the rectus abdominis and the mandibulohyoideus (his genio-hyoideus). Avery and Tanner (1964) use a specimen of *Sceloporus magister* for comparison with *Sauromalus*. Snyder (1962) illustrated the hind leg of *Sceloporus* in his discussion of muscle grouping and development in relation to lizard bipedalism. In his paper on the anatomical ratios of lizard limbs, Snyder (1954) used *Sceloporus* as an example of persistent quadrupedality.

The paucity of information on the muscular anatomy of one of the largest genera of New World lizards was the impetus for this study. The primary concern of the study was the description of the myology of the entire body of *Sceloporus clarki*. Comparative dissections of other species of *Sceloporus* were made. Comparisons were also made with descriptions of the myology of other iguanids.

I wish to thank Dr. Hugo Rodeck, director, and Dr. T. Paul Maslin, curator of zoology, of the Museum of the University of Colorado for permission to dissect specimens from the herpetologieal collections. Funds for the collection of specimens were provided by the Kathy Lichty Fund and Grant #GB 2362, National Science Foundation made to Dr. T. Paul Maslin. The figures were drawn by Miss Susan George.

This manuscript has been reviewed by Drs. W. W. Tanner, H. M. Smith, and D. F. Avery. Their comments and suggestions are greatly appreciated.

MATERIALS AND METHODS

The species used for the basic dissections was *Sceloporus c. clarki* Baird and Girard. Sufficient specimens were dissected to note variation found within a species. *Sceloporus magister*, a closely related species (Lowe, Cole and Patton, 1967), was selected for comparative purposes. The phylogenetic tree postulated by Smith (1939) was used to select several other species of *Sceloporus* for comparative examination. These species were used to determine at what level of consanguinity, anatomical differences, if any, occurred.

Speciment of *Sceloporus c. clarki* examined were UCM 13289, 34095, 34099, 34183, 34184, 34185, 34202, 34215, 34216, 34217, 34218, 34157, 34158, 34159, 35160, 34179, 34180. Five unregistered specimens were also dissected.

Specimens of other species of *Sceloporus* used for comparative purposes were *Sceloporus magister* Hallowell UCM 30178; *Sceloporus poinsetti* Baird and Girard UCM 34132; *Sceloporus v. variabilis* Wiegmann UCM 28778, 28782; *Sceloporus malachiticus smargadinus* Boucourt UCM 24523, 24525; *Sceloporus undulatus erythrocheilus* Maslin UCM 17414, 17442; *Sceloporus grammicus disparilis* Stejneger UCM 20034; *Sceloporus chrysostictus* Cope UCM 16511, 16548.

All specimens had been fixed in 10% formalin and stored in 70% ethanol.

Myology

The basic description following the muscle name is that of the condition found in *Sceloporus clarki.* Any deviation from this condition which was found in other species of *Sceloporus* dissected is then noted. Comparisons were then made with the published descriptions and illustrations of other iguanid lizards. The genera used for comparison were *Iguana* (Mivart, 1867; Romer, 1922; Haines, 1934, 1936; Howell, 1936, 1938; and Evans, 1939), *Phrynosoma* (Sanders, 1874; Jenkins and Tanner, 1968), *Ctenosaura* (Oelrich, 1956), *Sauromalus* (Avery and Tanner, 1964) and *Crotaphytus* (Robison and Tanner, 1962). Only those muscles which varied within the genus *Sceloporus* or between *Sceloporus* and other iguanids are included in the present account.

Muscle nomenclature used here is based primarily on that of Romer for the body musculature and Edgeworth for the musculature of the head.

Throat and Hyoid Musculature

Depressor palpebrae inferioris

Origin: from the floor of the orbit.

Insertion: into the whole of the lower eyelid.

This is an extremely thin and diffuse set of fibers found in the lower eyelid. No levator palpebrae superioris was found. Of the other studies, this muscle was noted only in *Ctenosaura.*

Intermandibularis

This is a thin sheet of muscle which lies on the ventral aspect of the lower jaw over the hyoid musculature. A varying number of fibers insert into the skin of the gular region. The muscle is divided into an anterior and posterior portion. The anterior portion is designated the intermandibularis anterior profundus, since it appears to be homologous to the deep portion of the intermandibularis anterior in those genera in which the intermandibularis has three slips. The fibers of this muscle lie perpendicular to the long axis of the body.

Intermandibularis anterior profundus

Origin: from the medial side of each dentary.

Insertion: into the midventral fascia.

In this genus the only differentiation between the anterior and posterior slips of the intermandibularis is the unmasked origin of the anterior profundus from the ramus. Its origin lies between that of the mandibulohyoideus and the genioglossus.

The intermandibularis anterior superficialis is not present in any species of *Sceloporus* examined. A narrow band of this muscle is present in *Crotaphytus, Sauromalus* and *Ctenosaura.* In *Phrynosoma,* the muscle appears to be fairly broadly developed.

Intermandibularis posterior

Origin: from the latero-ventral to lateral surface of the posterior half of the mandible.

Insertion: into the midventral fascia.

The anterior portion of the muscle comes to the surface of the throat by a varying number (3-7, usually 5-6) of slips which interdigitate with the mandibulohyoideus 1. The number of interdigitations is usually asymmetrical for an individual. The posterior portion comes from the lateral surface of the jaw, from the fascia covering the pterygomandibularis and also directly by a tendon from the lateral surface of the ramus between the pterygomandibularis and the insertion of the depressor mandibularis. In many specimens the muscle is composed only of fascia in the center so that the body of the hyoid and the base of the lingual process are visible through the fascia. This window of fascia occurs at the posterior boundary of the intermandibularis posterior. The fibers of the constrictor colli go to the midline just posterior to the window. In cases where this window was not present, it was very difficult to differentiate this muscle from the constrictor colli.

In the specimen of *magister* examined in the course of the dissection the intermandibularis posterior and constrictor colli appeared as one sheet of muscle. There also was no great division between the two portions of the intermandibularis. Avery and Tanner (1964, p. 15) state that the specimen of *magister* which they examined had a broad separation between the two portions of the intermandibularis. In *variabilis* the intermandibularis posterior was very thin and composed of fascia over the entire ventral surface of the jaw while the anterior portion was very well developed and several fibers thick. In *grammicus* there was a window of fascia over the hyoid body. In *poinsetti* the posterior was thinly developed while the anterior was heavily developed. In *chrysostictus* there was no differentiation between the posterior and the constrictor colli. This is also the case in *undulatus.*

In *Crotaphytus* it was stated (Robison and Tanner, 1962) that the anterior profundis and posterior portions were not easily separated except by origin as in *Sceloporus.* But, the constrictor colli was separated from the posterior margin of the intermandibularis posterior by a band of fascia. There are three or four interdigitations of the posterior section with the mandibulohyoideus I. In *Sauromalus* the posterior is a narrow band of muscle which is separated from both the anterior section of the muscle and the constrictor colli by bands of fascia. In *Ctenosoura* the posterior section is broad and in contact with the constrictor colli. In *Iguana* the intermandibularis is heavily developed in conjunction with the dewlap. In *Phrynosoma* the intermandibularis group is well developed, but Sanders mentions no interdigitations of the posterior with the mandibulohyoideus I.

Constrictor colli

Origin: from the cervical portion of the dorsal aponeurosis.

Insertion: into the midventral fascia.

This is the thin sheet of muscle which covers the side of the neck and the posterior portion of the throat and hyoid. It is superficial to the depressor mandibulae group, the omohyoid, episterno-cleido-mastoid, episternohyoid and the deep neck muscles. The muscle is usually so broadly developed as to cover part of the temporal fossa. Some *clarki* specimens had fibers inserting into the surface fascia of the episternohyoid superficialis.

In *poinsetti* the constrictor colli was broadly developed but became tendinous before reaching the midline. In *undulatus* the constrictor colli was connected to the episternohyoideus but was not as broad as in *clarki*. In *variabilis, malachiticus,* and *grammicus,* it was present only as a narrow band across the throat, widely separated from the intermandibularis posterior, and covering only a portion of the omohyoid and episternohyoideus superficialis.

The constrictor colli is present as a narrow band also in *Phrynosoma*, *Crotaphytus*, *Sauromalus,* and *Ctenosaura.* In *Iguana* it is more heavily developed in conjunction with the throat fan and is continuous with the intermandibularis posterior.

Mandibulohyoideus I

Origin: on the medial surface of the posterior half of the ramus.

Insertion: to almost the entire length of the first ceratobranchial.

This muscle lies immediately deep to the intermandibularis posterior, lateral to the hyoglossus, medial to the pterygomandibularis and superficial to the branchiohyoideus. The intermandibularis rises to the surface through interdigitations with this muscle.

Mandibulohyoideus II

Origin: by a thin, broad band of fascia from the dentary symphysis and the adjacent bone.

Insertion: on the anterior portion of the first ceratobranchial near the body of the hyoid.

The insertion may extend down the anterior half of the first ceratobranchial on the ventral and ventrolateral surfaces.

Hyoglossus

Origin: from ceratobranchial I.

Insertion: to the lingual process of the hyoid and the fleshy base of the tongue.

This muscle is deep to the posterior portion of the genioglossus and superficial to the brachiohyoideus. It occupies the space between the ceratohyal and ceratobranchial I.

Genioglossus

Origin: from the anterior third of the mandible anterior to the origin of mandibulohyoideus I.

Insertion: on the first ceratobranchial near the body of the hyoid and also by fascia into the covering fascia of the dorsal surface of mandibulohyoideus I.

The origin is deep to that of mandibulohyoideus II and the insertion is superficial to the hyoglossus.

Branchiohyoideus

Origin: from the center of the ceratohyal.

Insertion: to the posterior portion of ceratobranchial I.

This small muscle fills almost the entire space between the hyoid bones except for the most medial portion.

In *Crotaphytus* and *Sauromalus* this is a much smaller muscle which is confined to the lateral portion of the space between the hyoid bones. It is fairly broad in *Ctenosaura* but does not fill the entire space.

Constrictor laryngi

Origin: from the midventral line of the cricothyroid cartilage.

Insertion: to the middorsal line of the epiglotic cartilage.

Dilator laryngi

Origin: from the base of the cricothyroid cartilage.

Insertion: to the dorso-lateral surface of the posterior process of the cricothyroid cartilage.

Episterno-cleido-mastoideus

Origin: from the ventral surface of the clavicle, from the ventral surface of the sternum by a heavy, broad band of fascia which does not develop muscle fibers until it passes over the clavicle and, usually, a slip of varying size which rises from the fascia of the episternohyoideus superficialis.

Insertion: to back of quadrate and lateral surface of exoccipitals.

The origin is superficial to that of the omohyoid. The muscle lies deep to the constrictor colli and the depressor mandibularis group. In the other species of *Sceloporus*, except in the specimen of *grammicus* which was examined, there was also a slip from the surface of the episternohyoideus superficialis. However, the variability of the development of this muscle in *clarki* would suggest that the condition in the single specimen of *grammicus* might not always be the case.

Crotaphytus may have a slip from the sternohyoideus superficialis, depending on the species. *Ctenosaura* has a doubleheaded episterno-cleidomastoideus. *Sauromalus* has no carry-over of muscle fibers from the sternohyoideus superficialis. Avery and Tanner reported a single head in the specimen of *Sceloporus magister* they dissected.

Omohyoideus

Origin: from the scapula and the lateral part of the clavicle.

Insertion: into the body of the hyoid and the whole of ceratobranchial I.

This is a straplike muscle, triangular in cross-section, which is deep to the intermandibularis posterior and constrictor colli, medial to mandibulohyoideus I and superficial to the insertion of the episternohyoideus superficialis. The origin is covered by that of the episterno-cleido-mastoideus. In one case the omohyoid took part of its origin from the midline fascia superficial and lateral to the episternohyoideus superficialis. In another case this muscle was markedly asymmetrical in its development. In some cases a raphe was present in the center of the muscle at the level of the raphe marking the insertion of the episterno-hyoideus profundus into the fibers of the episternohyoideus superficialis, which lies medial of the omohyoid.

This muscle was well developed in most of the other species of *Sceloporus*. In *undulatus* and *chrysostictus* it was thin, straplike and rectangular in cross-section. In *chrysostictus* the muscle was elongated, as were the episternohyoideus and episterno-cleido-mastoideus, due to the lengthening of the neck and hyoid apparatus in this species.

The investigators of *Crotaphytus* and *Sauromalus* did not find the omohyoid to be distinguishable from the episternohyoideus. Sanders illustrates a well-developed omohyoid in *Phrynosoma*. In *Ctenosaura* the muscle was present and rectangular in cross-section.

Episternohyoideus superficialis

Origin: by a thin, broad fascia from the interclavicle and the fascia covering the pectoralis.

Insertion: onto almost the entire length of ceratobranchial I.

The origin of this muscle is superficial to the pectoralis and deep only to the skin. The insertion is immediately deep to the omohyoid. The body of the muscle runs parallel to the ceratobranchial II and is attached to it by a fascia but no muscle fibers. A varying number of lateral fibers are incorporated into the episterno-cleidomastoideus. In most specimens of *clarki* only one slip of this muscle is present.

Episternohyoideus profundus

Origin: from the midline fascia and interclavicle.

Insertion: into the dorsal surface of the episternohyoideus superficialis by a discernible raphe.

This muscle is either only occasionally present or very difficult to divide from the superficialis.

In *magister*, *undulatus*, and *malachiticus*, only the superficialis was present. In one specimen of *variabilis* the muscle was single. In the other, the superficialis inserted onto the proximal portion of ceratobranchial I and completely enveloped ceratobranchial II. In *grammicus* the muscle had a single origin but a double insertion. One insertion was to the body and proximal portion of ceratobranchial I, while the other slip was to the most distal portion of ceratobranchial I. In *poinsetti* the profundus extends to the dorsal surface of ceratobranchial I. The superficialis extends to the ventral surface of the proximal portion of ceratobranchial I with additional fibers to the medial and lateral surfaces. In *chrysostictus* it was single with a heavier concentration of fibers to the proximal section of the first ceratobranchial. In this species the elongation of the neck has caused the ceratobranchial I to lie parallel to the ramus of the mandible for a longer distance than is found in other species of *Sceloporus*. This elongation of the ceratobranchial has caused the episternohyoideus to assume the shape of a parallelogram rather than the fan-shape found in other species.

In *Crotaphytus* and *Sauromalus* this muscle was found to have a midventral fold which causes it to have the appearance of two muscles. Sanders illustrates (1874, fig. 1) a narrow, bandlike episternohyoideus.

Jaw Musculature

Levator anguli oris

Origin: from the squamosal, postorbital and dorsal portion of the tympanic crest.

Insertion: into the skin of the corner of the jaw and the mundplatte.

This muscle lies directly below the heavy infratemporal fascia. It is superficial to the adductor mandibularis externus. The mundplatte into which this muscle inserts, is a heavy sheet of fascia which arises on the postorbital bar and inserts onto the articulare. The mundplatte is the only fascial sheet in *Sceloporus* which is underlain by a fold of skin.

In *Ctenosaura* and *Crotaphytus* the levator also takes origin from the medial surface of the infratemporal fascia.

Adductor mandibularis externus

Origin: from the posterior portion of the postorbital and squamosal.

Insertion: onto the lateral surface of the posterior third of the ramus of the mandible.

This is the large muscle at the angle of the jaw. It is dorsal to the pterygomandibularis, anterior to the depressor mandibularis group and deep to the levator anguli oris. It is covered by the temporal fascia and the levator anguli oris so that it is not visible directly. In *Sceloporus* it is not easily divided into the component elements and only two portions were found. Three were reported from *Ctenosaura*, *Crotaphytus* and *Sauromalus*.

Depressor mandibularis

Origin: from the dorsal aponeurosis.

Insertion: into the back of the mandible.

The group of depressor mandibularis muscles appears on the lateral surface of the head and neck. They lie deep to the constrictor colli, superficial to the episterno-cleido-mastoideus and axial muscles and anterior to the trapezius. In *Sceloporus* three muscle slips are separable. The anterior two are usually divided from the posteriormost and are termed the depressor mandibularis. The posterior section is usually called the cervicomandibularis in anatomical studies but could be called the depressor mandibularis posterior.

Depressor mandibularis anterior

Origin: from the back of the parietal and the very anterior portion of the dorsal aponeurosis.

Insertion: on the articulare.

If heavily developed, this muscle will mask the back half of the temporal opening. It extends posteriorly for a short distance from its origin then turns ventrad and lies along the posterior margin of the external auditory meatus. The muscle fibers are replaced by a tendon approximately at the middle of the auditory meatus which then passes below the tendon of insertion of the depressor mandibularis lateralis.

Depressor mandibularis lateralis

Origin: from the cervical portion of the dorsal aponeurosis.

Insertion: on the articulare.

The lateralis is much broader and thicker than the anterior slip. It extends ventrad from its origin and then turns anterior to its insertion. The insertion and ventral portion of the belly cover the posterior portion of the anterior slip.

Cervicomandibularis

Origin: from the dorsal aponeurosis at the level of the more posterior cervical vertebrae.

Insertion: in the fascia of the intermandibularis posterior and on the back of the ramus.

From the broad origin the fibers of the muscle extend ventrally and anteriorly to converge at the insertion. The breadth of origin and thickness of development are variable, but there did not seem to be any correlation between development and either size or sex. The development of the muscle ranged from a broad, straplike muscle to a thin sheet of fascia with a few muscle fibers scattered through it. In one individual it was not discernible. Its variability, posterior origin, and weak insertion would indicate that it is the weakest of the jaw depressors.

This muscle was similar in the other species of *Sceloporus*, except that in one specimen of *undulatus* the fascia of insertion was into the ventral midline at the level of the hyoid body.

Three section of this muscle were present in *Sauromalus*, *Ctenosaura*, *Phrynosoma*, *Iguana* and *Crotaphytus wislizeni* and *reticulatus*. *Crotaphytus collaris* is reported as having only two bundles which seem to be the anterior and lateral slips. According to Sanders the cervicomandibularis (his neuro-mandibularis) was a well-developed band which inserted onto the back of the mandible. Camp (1923, Fig. 45) indicates in *Phrynosoma* that the insertion was into the fascia of the central part of the intermandibularis posterior.

Shoulder Girdle Musculature

Trapezius

Origin: from the dorsal aponeurosis at the level of the posterior cervical and anterior dorsal vertebrae.

Insertion: onto the scapula by the overlying fascia.

The anterior portion of this muscle lies deep to the cervicomandibularis. The posterior portion is superficial to the latissimus dorsi and the axial musculature. In two specimens some fibers inserted into the lateral section of the clavicle next to the origin of the episterno-cleido-mastoideus.

Crotaphytus was also noted to have a partial insertion onto the clavicle. Sanders (1874) reported that the specimen of *Phrynosoma*, which he examined, had no trapezius. Jenkins and Tanner (1968) found a narrow trapezius in *Phrynosoma platyrhinos* and *douglassi*.

Latissimus dorsi

Origin: from the dorsal aponeurosis of most of the dorsal vertebrae.

Insertion: on the processus latissimus dorsi just below the head of the humerus between the scapular and coracoid heads of the triceps.

This is the largest of the superficial dorsal muscles. The posterior border is sometimes difficult to determine as fibers running at the same angle are present in the fascia to the level of the sacrum. Its borders are further disguised by a heavy concentration of melanophores which occur in the surface fascia of the entire body.

In *poinsetti* the latissimus dorsi was only one fiber thick so that the iliocostalis and the tendons of the spinalis and semispinalis were visible. The insertion fibers appeared to be as heavy, however.

In *Phrynosoma*, Sanders (1874) found the latissimus to be only a narrow band arising from the level of the spines of the third and fourth dorsal vertebrae. Jenkins and Tanner (1968) reported a broad latissimus dorsi originating from the superficial dorsal fascia.

Serratus dorsalis

Origin: by three slips from the cervical ribs.

Insertion: on the medial surface of the scapula dorsal to the insertions of the serratus ventralis and subscapularis.

These muscles, which form part of the sling by which the anterior limb is attached to the body, are visible when the lattissimus dorsi and trapezius are cut and the scapular elements are pulled away from the body.

In *Phrynosoma* Sanders (1874) found only two slips to the dorsal section of the serratus. Jenkins and Tanner (1968) reported three slips of this muscle.

Serratus ventralis

Origin: from the middle of the first thoracic ribs.

Insertion: on the posterior margin of the scapula posterior to the insertions of the serratus dorsalis and subscapularis.

In *Crotaphytus* the serratus ventralis had two slips rather than one large muscle. In this case they also took origin from the cervical ribs.

Subscapularis

Origin: from the medial surface of the suprascapula and scapula ventral to the insertion of the serratus ventralis.

Insertion: onto the proximal, medial surface of the humerus.

In *Crotaphytus*, two slips of this muscle were reported.

Biceps brachii

Origin: originates by two broad, flat tendons from the ventroposterior margin of the coracoid.

Insertion: by a single tendon into the tendon of insertion of the humeroantebrachialis.

This is the largest muscle of the anterior surface of the humerus. The anterior tendon develops a small flat belly of muscle which runs almost to the shoulder joint which it crosses as a broad tendon just posterior to the insertion of the pectoralis. This becomes the lateral belly of the biceps. The tendon of the medial belly remains tendinous from its origin, over the shoulder joint, until the belly develops approximately one-third of the way down the humerus. The two bellies join in the distal third of the brachium and a single tendon moves over the elbow to its insertion.

Robison and Tanner (1962, p. 16) consider this unit to be composed of two muscles, after Mivart's (1867) work on *Iguana*. The anterior belly is considered to be a separate muscle—the brachialis inferior. Romer (1924) considers the muscle to be single but doubleheaded. Sanders considers the muscle in *Phrynosoma* to consist of the biceps and the brachialis anterior. The inclusion of muscle fibers in the anterior head as it passes over the coracoid is not mentioned elsewhere.

Coracobrachialis brevis

Origin: from the majority of the medial portion of the coracoid.

Insertion: to the proximal two-thirds of the medial surface of the humerus.

The origin is deep to the tendons of origin of the biceps brachii. In *Iguana* Howell (1936) found two slips of this muscle. In *Phrynosoma* the insertion is to nearly the entire length of the humerus.

Triceps brachii

This is the large muscle on the posterior surface of the brachium. The origins of the various slips are well separated, but the insertion is by a common tendon which passes over the elbow to insert onto the olecranon of the ulna and which contains the sesamoid ulnar patella.

Lateral humeral head of the triceps

Origin: from the lateral surface of the proximal half of the humerus.

Insertion: into the common tendon.

This head of the triceps lies lateral to the scapular head and joins with it halfway down the brachium.

Medial humeral head of the triceps

Origin: from the medial surface of the humerus about halfway down the shaft.

Insertion: into the common tendon.

This head of the triceps lies medial to the scapular head. It joins the other heads of the triceps just before the tendon crosses the elbow joint.

Scapular head of the triceps

Origin: by a heavy tendon from the posteroventral corner of the external surface of the scapula.

Insertion: into the common tendon.

This head of the triceps joins the lateral humeral head at approximately the middle of the brachium. It is joined to the coracoid head by a sling tendon in all examined species of *Sceloporus*. This tendon was not noted in *Crotaphytus* and *Sauromalus* but was noted to be strongly developed in *Iguana* by Howell (1936).

Coracoid head of the triceps

Origin: by a strong tendon either directly from the posterior portion of the medial surface of the coracoid or from the sternoscapular ligament.

Insertion: into the common tendon.

This is the most variable head of the triceps. In *clarki* the head varied from strongly developed to completely degenerated. In the case where the belly was completely degenerated the tendon was still present. If the belly is present, it develops at the level of the insertion of the latissimus dorsi. The slip lies medial to the scapular head and superficial to the medial humeral head. The sling tendon was well developed in *magister*, *chrysostictus* and *undulatus*. It was rather weakly developed in *grammicus* and *malachiticus*.

In *Phrynosoma* and Mivart's (1867) *Iguana* account, the inner (coracoid) head of the triceps receives a tendon from the latissimus dorsi, very close to the latter's insertion. From the illustration, this appears to be the sling tendon.

In *Sceloporus* the sling tendon is connected with a subscapular ligament and together they form a complicated set of tendons. The subscapular ligament usually has three points of connection. The most lateral point is that of a strong but narrow tendon which arises from the posterior corner of the coracoid. The tendon of origin of the coracoid head of the triceps arises from this tendon a few millimeters from its origin. The tendon runs medially where an anterior tendon extends forward to the fascia of insertion of the levator scapula profundus. The original tendon then continues medially to the anterior portion of the costocoracoid muscle. The three points of connection then are the posterior corner of the coracoid, the back of the levator scapulae profundus, and the sternum, by the fascia of the costocoracoid.

Variations of this basic pattern were specimens of *clarki* in which the coracoid head arose directly from the coracoid in conjunction with the subscapular ligament, and specimens of *undulatus* in which an additional slip of muscle from the center of the first abdominal rib enters the costocoracoid where that muscle becomes tendinous and enters the subscapular ligament. In *grammicus* the ligament proceeds directly from the sternum to the coracoid without sending an extension to the levator scapulae profundus. This species also has the extra slip of the costocoracoid.

Howell (1936, p. 200), in his dissection of *Iguana*, notes a similar, but not identical, situation:

"Thus, in *Iguana*, the scapulo- and coracotriceps arise from a continuous sling or loop, suspended laterally between scapula and humerus and medially between sternum, coracoid and scapula."

In the dissections of *Crotaphytus* and *Sauromalus*, no mention is made of the sling tendon between the scapular and coracoid heads of the triceps but in their discussion of the costocoracoid, Robison and Tanner (p. 20) note that "the costocoracoid . . . inserts, just dorsal to the midregion of the first subscapularis, on a ligament which extends between the inner surface of the sternum . . . and the anterior border of the scapula."

Costocoracoid

Origin: from the medial portion of the first abdominal rib and from the lateral margin of the posterior half of the sternum.

Insertion: to the back of the coracoid by the sternoscapular ligament.

This muscle consists of fibers which arise from the first rib and the sternum posterior to the point from which the ligament extends to the back of the coracoid and a broad, flat sheet of fascia anterior to the point of attachment of the ligament.

In *grammicus* and *undulatus* there is also a slip from the center of the first abdominal rib into the costocoracoid just before it becomes tendinous.

AXIAL MUSCULATURE

Rectus abdominis superficialis

Origin: on the anterior margin of the pubis.

Insertion: on the last abdominal rib posterior to the origin of the pectoralis.

This is the large superficial muscle of the belly. The identity of the lateral boundaries of of the rectus is lost in the middle of the belly as fibers from the rectus are incorporated into the obliquus externus. In *Sceloporus* there are three inscriptions in the body of the muscle.

Rectus abdominis internus

Origin: from the symphyseal area of the pubis.

Insertion: into the midventral line or, in some cases, onto the last abdominal rib.

In *clarki* the rectus internus inserts into the midventral line to the level of the xiphisternal ribs, resulting in a triangular muscle. In other species the muscle inserts into only the posterior section of the midventral line. In *grammicus* and one specimen of *chrysostictus* the insertion was directly onto the xiphisternal ribs.

Obliquus externus

Origin: from the middle of the body of the dorsal ribs.

Insertion: into the midventral line of the dorsal surface of the rectus abdominis.

The direction of the fibers is ventral and posterior. Since fibers of the muscle do not arise from the posterior dorsal vertebrae, there remains a triangular space in front of the hind leg in which the viscera is covered only by the peritoneum, the thin sheets of the obliquus internus, and the transversus abdominis.

In some individuals the slips retain individual identity as they arise from the ribs almost to their insertion posterior to the point where the posterior margin of the latissimus dorsi crosses the level of the insertion of the obliquus internus. This tendency was also noted in *magister*.

MUSCULATURE OF HIND LIMB

Ambiens

Origin: from the anterior surface of the femur near the head below the insertion of pubo-ischio-femoralis internus.

Insertion: onto the patellar capsule and the head of the tibia.

This muscle covers the leading edge of the thigh. In *Sceloporus* the muscle is single and simple. The origin is covered by the origin of the femorotibialis.

Femorotibialis

Origin: broadly from the head of the femur and the fascia of the pubo-ischio-femoralis internus.

Insertion: broadly to the head of the tibia, just proximal to the insertion of the flexor tibialis internus superficialis.

This muscle is visible on the ventral surface of the thigh posterior to the ambiens and anterior to the pubo-ischio-tibialis. It extends diagonally from its origin beneath the pubo-ischio-tibialis and the insertion of the adductor.

Pubo-ischio-tibialis

Origin: from the puboischiadic ligament

Insertion: onto the tiba by a broad tendon which it has in common with the flexor tibalis externus.

This is the largest muscle of the ventral surface of the thigh. The insertion is on the anterior surface of the tibia between the bodies of the tibialis anterior and the extensor digitorum communis several millimeters below the patella. This muscle lies directly below the femoral pores and bears their imprint in preserved specimens.

In *poinsetti* the muscle is less heavily developed and has a definite slip between the main portion and the flexor tibialis externus. It inserts into the broad tendon of the main part of the muscle by a thin band which remains visible in the fascia across to the tibia. In *malachiticus* the common tendon enters the tibia just below the knee joint.

Flexor tibialis externus

Origin: from the tubercle of the ischium and the ilioischiadic ligament.

Insertion: into the body of the pubo-ischio-tibialis before it becomes tendinous.

This muscle occupies the posterior border of the thigh. In all species examined the flexor enters into the pubo-ischio-tibialis before that muscle crosses the knee, although there is some variation in the distance above the knee the junction occurs. In some specimens of *clarki* some of the more posterior fibers of the flexor enter the tendon rather than the muscle. In *undulatus* the more posterior fibers give rise to a small, independent tendon which crosses the knee posterior to the larger tendon.

In *Phrynosoma* and *Iguana* the flexor tibialis externus crosses the knee independently.

Flexor tibialis internus

Origin: from the ilio-ischiadic ligament deep to the origin of the flexor tibialis externus.

Insertion: by three tendons on the head of the tibia.

The flexor tibialis internus splits into three bellies at the level of the head of the femur. The largest belly inserts broadly to the head of the tibia immediately deep to the common tendon of the pubo-ischio-tibialis and the femorotibialis. Of the two smaller bellies, one belly develops a long, narrow tendon two-thirds of the way down the thigh which inserts into the posterior surface of the head of the tibia. This is the deepest slip. The third slip is slightly posterior to the other two and develops a tendon of insertion just proximal to the knee joint.

Popliteus

Origin: from the postero-lateral surface of the head of the fibula.

Insertion: into the tendon of the flexor hallucis longus.

In *Sceloporus* the popliteus is an extremely short muscle which arises directly from the bone. The fibers wrap around the tendon of the flexor hallucis longus. This is almost the mammalian condition rather than the normal reptilian condition of a well-developed popliteus.

Gastrocnemius

Origin: the lateral head from the head of the fibula, the medial from the head of the tibia.

Insertion: by a common tendon into the plantar aponeurosis.

In *Sceloporus* this muscle is two-headed and two-bellied but has a single insertion and will be considered as a single muscle. In some cases the muscle has been considered as two muscles—the soleus and the gastrocnemius. There has been little agreement over which is which, but most recently George (1948) called the fibular head; the soleus.

Flexor digitorium brevus

Origin: from the tarsals and the plantar aponeurosis.

Insertion: to the ventral surfaces of the phalanges.

This muscle is superficial to the flexor digitorum longus. The palmar aponeurosis is present but is not as heavily developed as has been reported from other lizards. Also, there is no sesamoid bone found, although Cope (1892, p. 196) states that "In all the normal Lacertilia the tendons of the flexors of the digits are combined on the palm and the point of junction is occupied by a large, flat sesamoid bone."

DISCUSSION

Within the genus *Sceloporus*, or at least in the species examined, it can be seen that the myology is generally very constant. Those muscles which are constant within the genus are essentially those which are constant within the members of the family which have been examined.

Etheridge (1964) has indicated that *Sceloporus* is an advanced iguanid in comparison to other iguanid genera by virtue of osteological characters. Only a limited amount of myological comparison can be made because of the small number of myological studies available within the family.

The muscles in which the greatest variability occurred were the intermandibularis group, the constrictor colli, the episterno-cleido-mastoideus, the episternohyoideus, the coracoid head of the triceps, the costocoracoid, and the flexor tibialis externus. It will be noted that most of this variation is in the neck region.

The variation in the intermandibularis was used by Camp (1923) in the construction of his lizard classification. The results of the present study are not always in agreement with his conclusions. According to Camp, *Sceloporus* is one of the genera in which separation of the profundus and superficialis bundles of the intermandibularis anterior has occurred, and he states (p. 370) that "in the iguanids, *Callisaurus, Uma* and *Holbrookia*, alone, is the superficial layer absent." It was not noted in any of the species of *Sceloporus* dissected. According to Camp, the number of interdigitations of the intermandibularis posterior with the mandibulohyoideus I can be used for purposes of classification because they are regular and equal. In *clarki* alone, the number of interdigitations ranged from three to seven and usually were not the same in numbr for the two sides. Therfore, the use of this muscle for classification purposes in *Sceloporus* does not seem warranted. Camp's criterion of the primitive iguanid throat musculature is the condition in which there is a higher number of interdigitations of the posterior slip and the lack of or slight separation of the two slips of the anterior slip of the intermandibularis. In this respect, *Sceloporus* would maintain its place as one of the primitive iguanids.

The variable development of the constrictor colli is understandable if its broad development is associated with the throat fan of *Iguana*, while the absence of this throat flap in *Sauromalus* and the other ground iguanids is accompanied by a narrow constrictor colli. The variability of the muscle is less easily understood in the genus *Sceloporus*. It is broadly developed in the tree-living *clarki* and the rock-living *magister*. It occurs as a narrow band in *malachiticus* and *variabilis* which are quite far removed from each other according to Smith (1939). It apparently has no ecological and phylogenetic basis although more data are necessary to draw any conclusions. The behavior of the various species of *Sceloporus* is not well enough known to attempt any correlations.

The comparative development of the intermandibularis posterior and the constrictor colli seems to follow no patterns. In *Sceloporus*, the development of both muscles is variable with no relation between the two. In *Iguana* they are both heavily constructed. In *Sauromalus* both are narrow bands. In *Crotaphytus* and *Ctenosaura* the intermandibularis is broad and the constrictor colli is a narrow band.

The variation of the episterno-cleido-mastoideus seems to be without correlation. All species of *Sceloporus* examined, except *grammicus*, had a double-headed muscle. The variation in the size of the head from the episternohyoideus superficialis was negligible.

The muscles connecting the pectoral girdle and the hyoid apparatus show a great deal of variation. There is controversy among anatomists as to the nature and identification of these muscles. Camp illustrates (fig. 42-47, 53-65) the muscles he calls omohyoideus, sternohyoideus and sternothyreoideus and shows the great diversity of this group of muscles. The three are not always present simultaneously. Of the iguanids studied Camp indicates that all three were present in *Prynosoma*. Avery and Tanner (1964) in *Sauromalus* and Robison and Tanner (1962) in *Crotaphytus* reported that there was a single sheet of muscle folded back on itself at the midventral line. Camp illustrates this condition only in *Gerrhosaurus* (Fig. 63, 66). This folded condition has been reported for no other iguanids. If the muscle deep to the sternohyoideus superficialis is the episternothyreoideus, then the litter muscle is present in *poinsetti* and sporadic in *clarki*.

There is a graduation of conditions in *Sceloporus* of the episternohyoideus supericialis. In *magister*, *undulatus*, *malachiticus*, and most specimens of *clarki*, the muscle was single and inserted uniformly on the entire length of the first ceratobranchial. In *chrysostictus* there was a tendency for increase of fiber number to the proximal portion of ceratobranchial I. In one specimen of *variabilis* the muscle fibers were confined to the proximal portion of ceratobranchial I and had shifted part of their insertion to ceratobranchial II. Thus, concentration of fibers to the medial portion of the hyoid occurs in one of Smith's basic divisions of *Sceloporus* while the species with insertion into the whole of ceratobranchial I occur in the other branch. The tendency to develop the deeper slip is noted only for *clarki* and *poinsetti* which are fairly closely related, according to Smith, and would be an independent evolutionary trend.

Perhaps the most interesting of the muscle variations found in this investigation is the variability and the relationships of the subscapular ligament and the related muscles—the coracoid head of the triceps, the costocoracoid and the levator scapulae profundus. In the simplest condition the ligament seems to be the tendon of insertion of the costocoracoid in conjunction with a heavy fascia from the anterior edge of the sternum (Robison and Tanner, 1962). In *Iguana* (Howell, 1936), the tendon of the coracoid head of the triceps has entered into the ligament. Howell states that the ligament is presently in *Cyclura* but is less strongly defined, and does not elaborate. *Sceloporus* has added the further refinement of the inclusion of the levator scapulae profundus. At this stage of investigation the only attempt at correlation can be to say that the ligament seems to be more strongly and complexly developed in aboreal iguanids than in the ground dwellers.

The heavy development of the flexor tibialis externus in *Sceloporus* and its insertion on the body of the pubo-ischio-tibialis differ from other iguanids and other lizards. The heavy tibial flexors, which also act as femoral extensors, are used by Snyder (1954) in his analysis of the locomotor components in lizards. He indicates that *Sceloporus* is a natural quadruped, with no possibility of achieving the bipedality of other iguanids. The flexor tibialis externus was the most highly developed in *clarki;* less developed in *magister* and *poinsetti;* moderately developed in *undulatus* and *malachiticus*; and rather weakly developed in *variabilis.* Thus, the decidedly arboreal *clarki* has the most heavily developed flexor while it is rather weakly developed in the ground-dwelling *variabilis.* This muscle would be useful in a half-contracted position in the maintenance of posture on a tree trunk in a highly arboreal animal.

Avery and Tanner (1964, p. 28) have constructed a natural group of the genera *Sauromalus, Ctenosaura,* and *Dipsosaurus* which share the characteristics of (1) an intermandibularis anterior and posterior, (2) a single-headed episterno-cleido-mastoideus, (3) a depressor mandibularis group with three muscles and, (4) an herbivorous diet. They state that, in their opinion, *Sceloporus* differs only in that its species are omnivorous or carnivorous. Further work by Avery has indicated that *Sceloporus* is not very close to the iguanines (pers. comm.).

From the investigation herein described it would seem that the relationship of *Sceloporus* to these genera is not as close as is indicated.

1. *Sceloporus* lacks an intermandibularis anterior superficialis which is present in these genera and the posterior and anterior slips of the muscle are in contact rather than divided.

2. The episterno-cleido-mastoideus usually possesses a slip from the surface of the episternohyoideus superficialis and cannot be considered single-headed.

3. The third head of the depressor mandibularis group, or cervicomandibularis, is usually weakly developed and is sometimes absent.

The folded nature of the episternohyoideus in *Sauromalus* would seem to be a basic difference, as is the simple nature of the subscapular ligament.

These muscle differences would indicate that *Sceloporus* is not too closely related to *Sauromalus* and *Ctenosaura.* This is in agreement with Etheridge's findings (1964).

Crotaphytus is considered by Etheridge to be fairly closely related to the sceloporine lizards. The myology is more similar to that of *Sceloporus* than is that of *Sauromalus*, but there are still

TABLE I

List of abbreviations used in the figures.

a - ambiens
add - adductor
ame - adductor mandibularis externus
anu - ring muscle

bh - branchiohyoideus

c - cloaca
cb I - ceratobranchial I
cb II - ceratobranchial II
cc - constrictor colli
ch - ceratohyal
cm - cervicomandibularis
co - costocoracoid

dcm - caudae dorsalis

ecd - extensor communis digitorum
ecm - episterno-cleido-mastoideus
ehs - episternohyoideus superficialis
eo - obliquus externus

fdc - flexor digitorum communis
ft - femorotibialis
fte - flexor tibialis externus
fti - flexor tibialis internus

g - gastrocnemius
gg - genioglossus

hb - hyoid body
hg - hyoglossus

iap - intermandibularis anterior profundus
ifb - ischiofibularis
ip - intermandibularis posterior
it - ischiotibialis

lp - lingual process

mand - mandible
mh I - mandibulohyoideus I
mh II - mandibulohyoideus II
mh II - mandibulohyoideus III

oh - omohyoideus

pb - peroneus brevis
pect - pectoralis
pifc - pubo-ischio-femoralis
pl - peroneus longus
pt - pubo-ischio-tibialis
ptery - pterygomandibularis

ra - rectus abdominis

sb - subscapular ligament
st - sternum

ta - tibialis anterior
tlsp - tendon to levator scapulae profundus
toc - tendon to origin of coracoid head of triceps
tp - transversus perinei

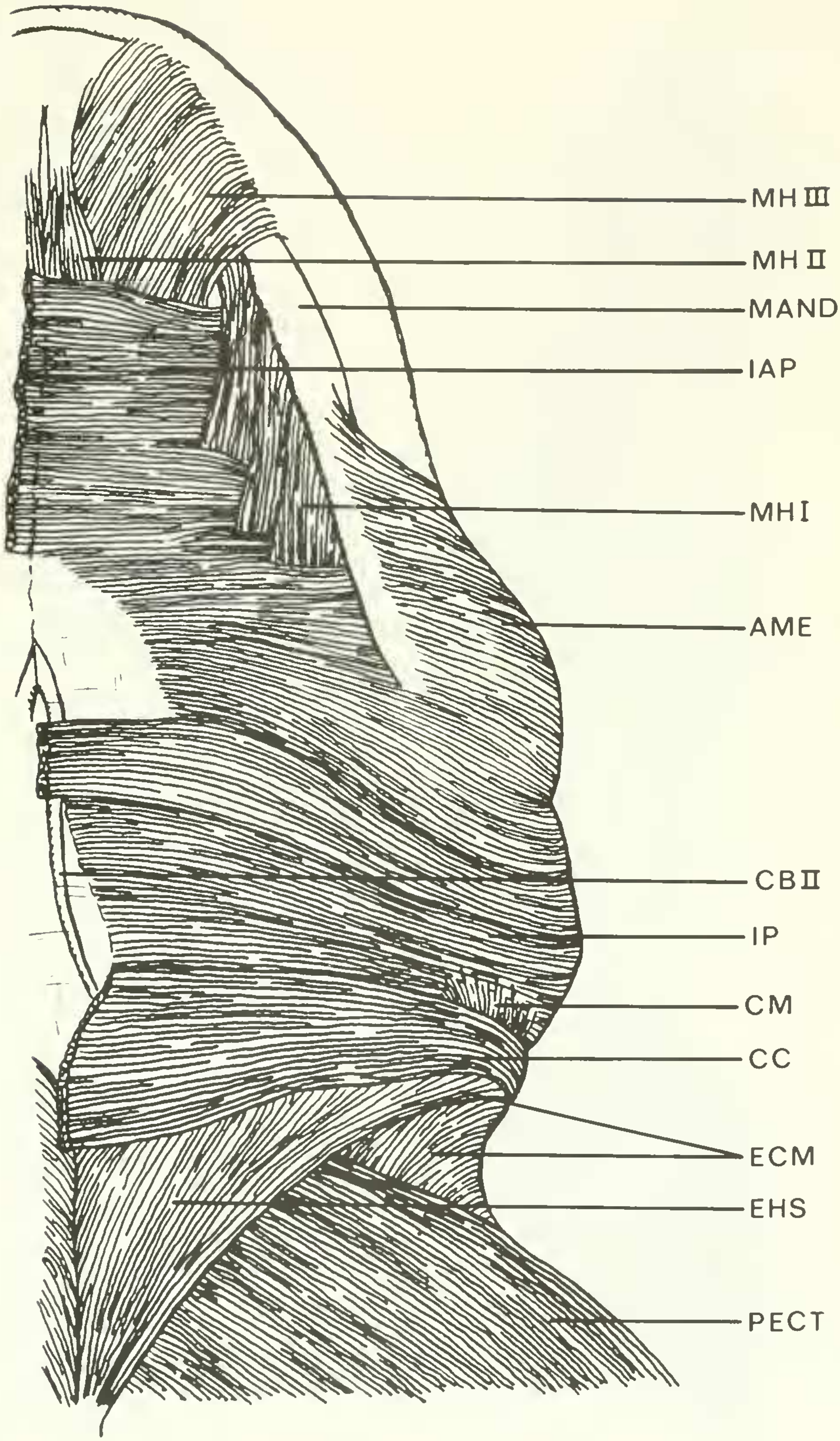

Fig. 1. Ventral view of throat, superficial musculature.

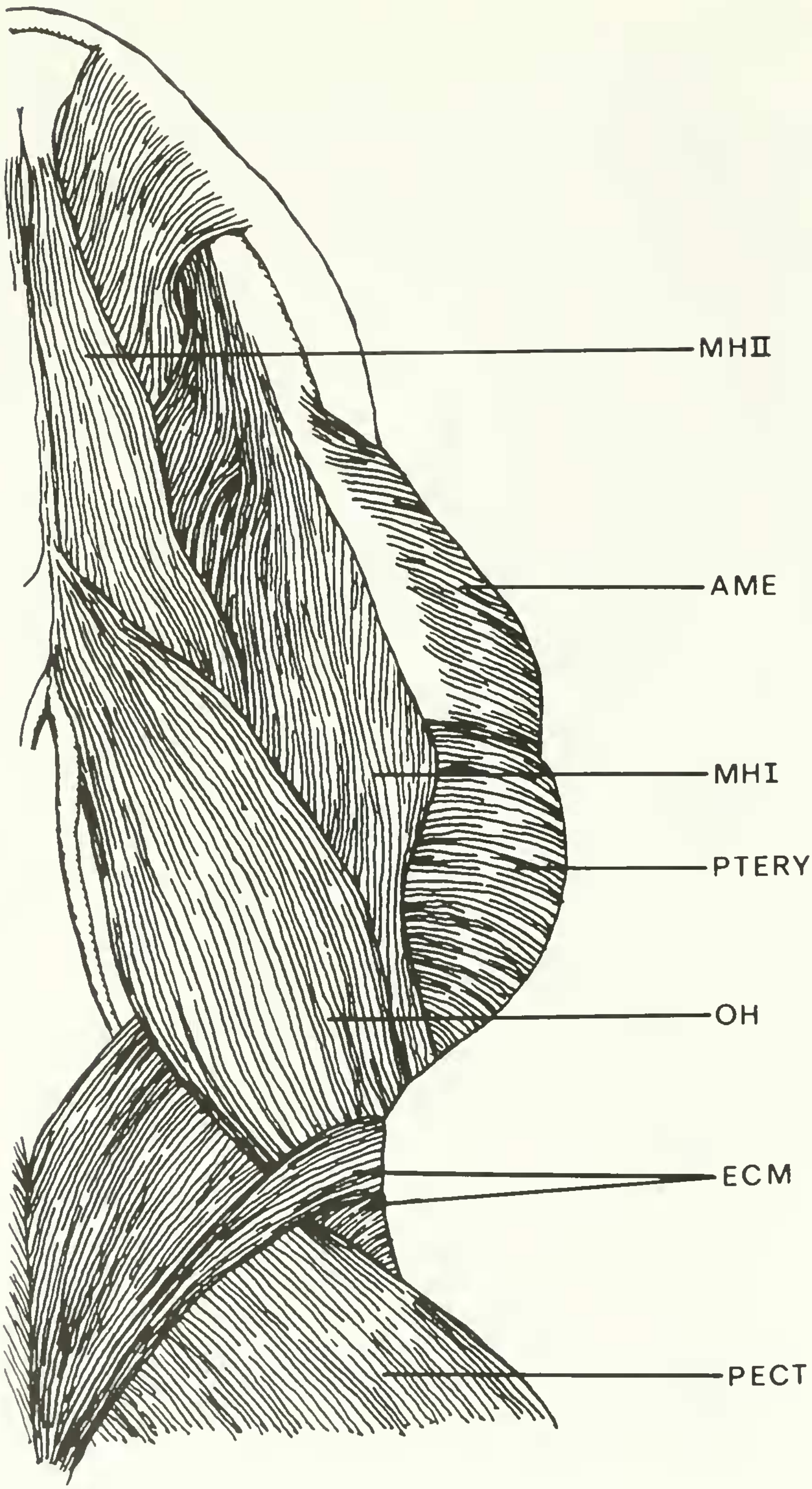

Fig. 2. Ventral view of throat, second layer.

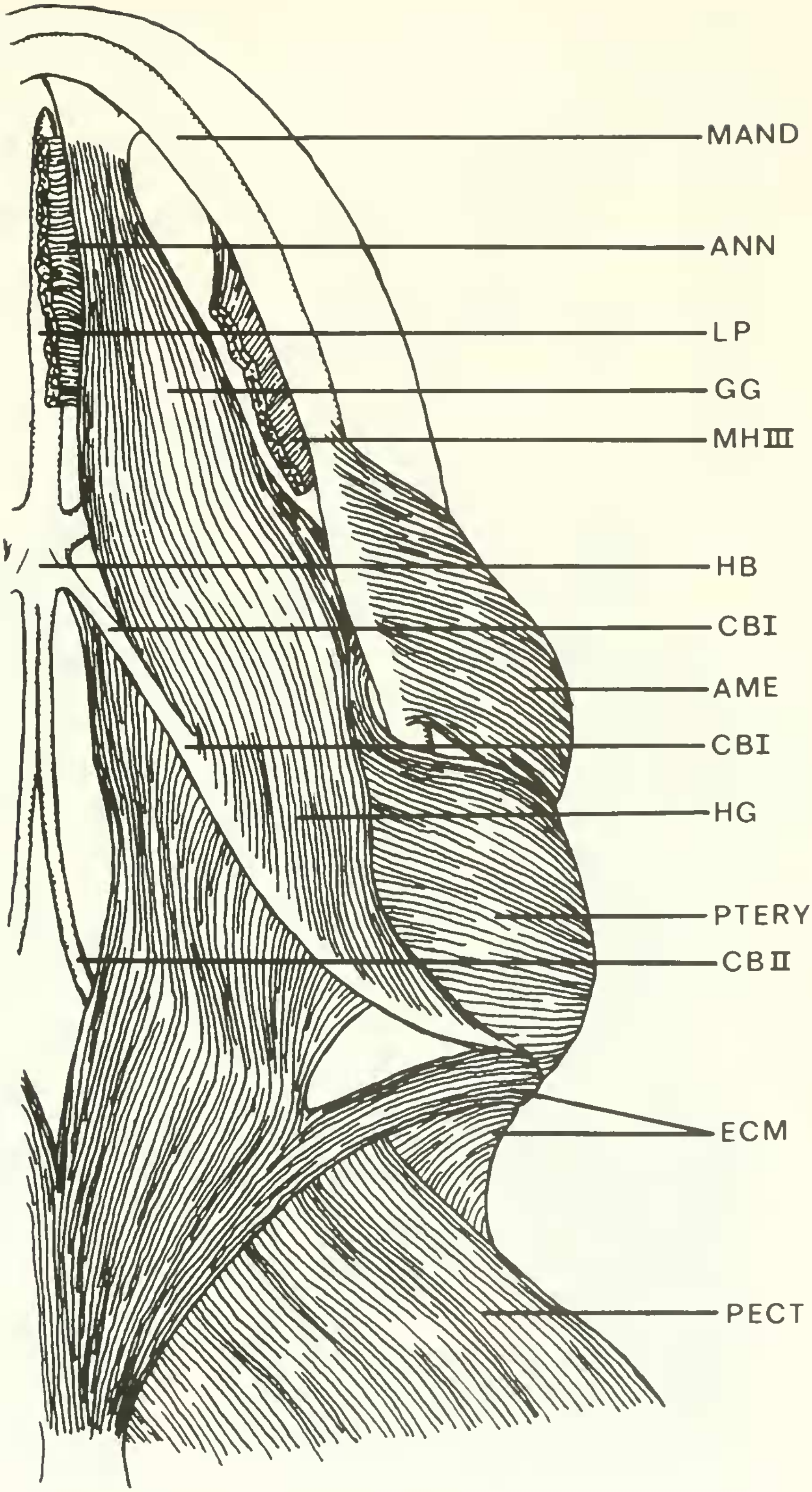

Fig. 3. Ventral view of throat, third layer.

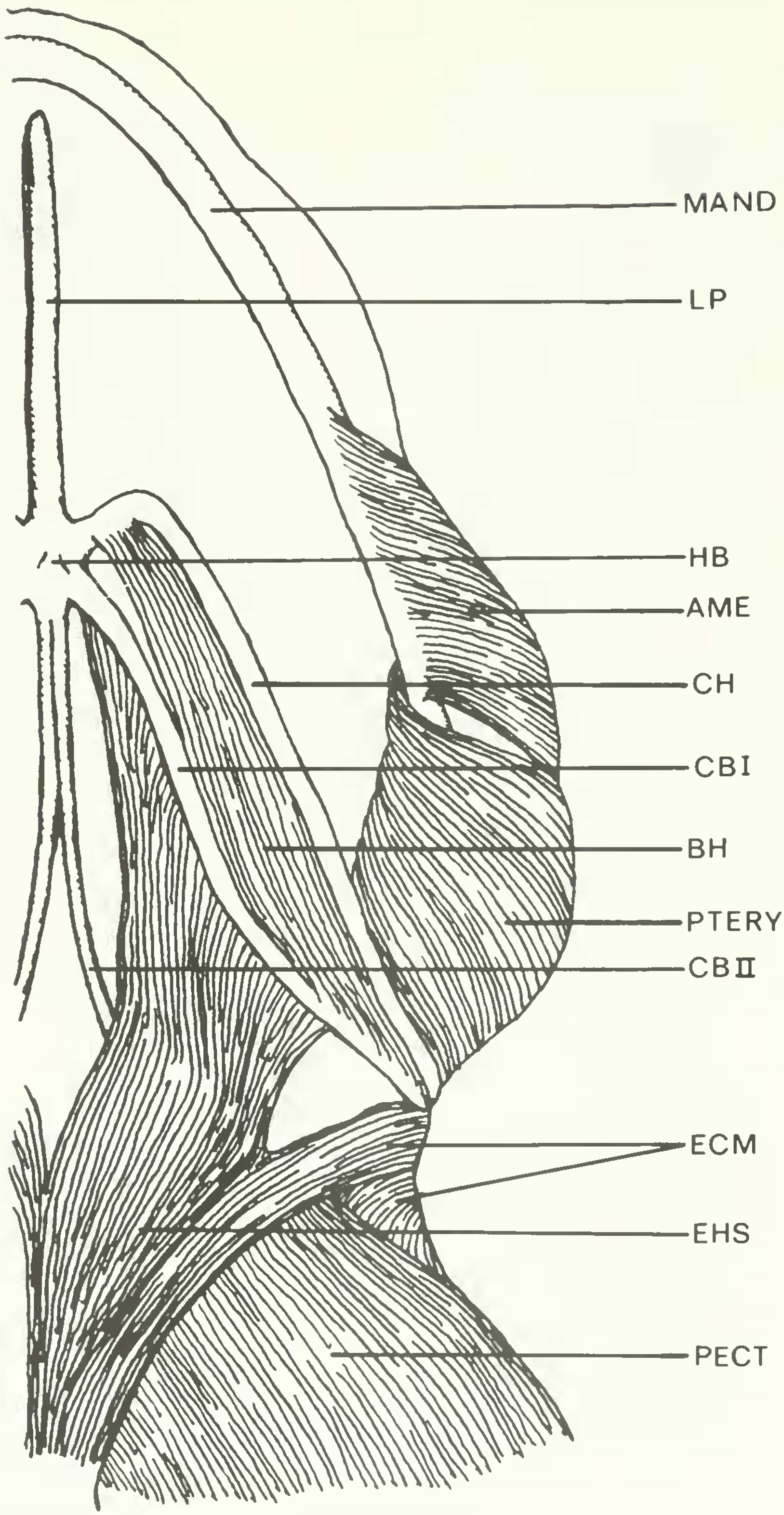

FIG. 4. Ventral view of throat, deepest musculature.

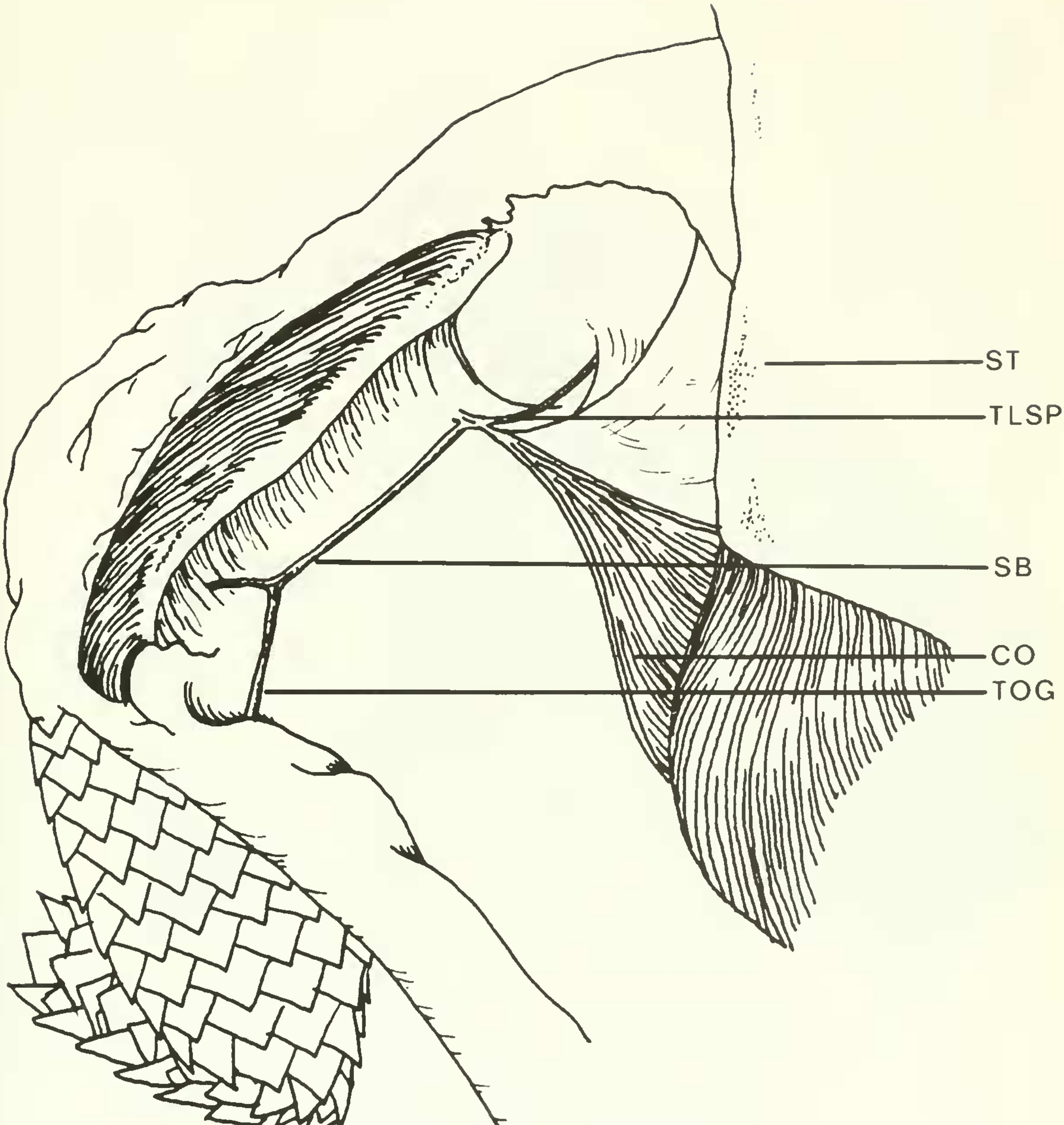

Fig. 5. Subscapular ligament and associated muscles.

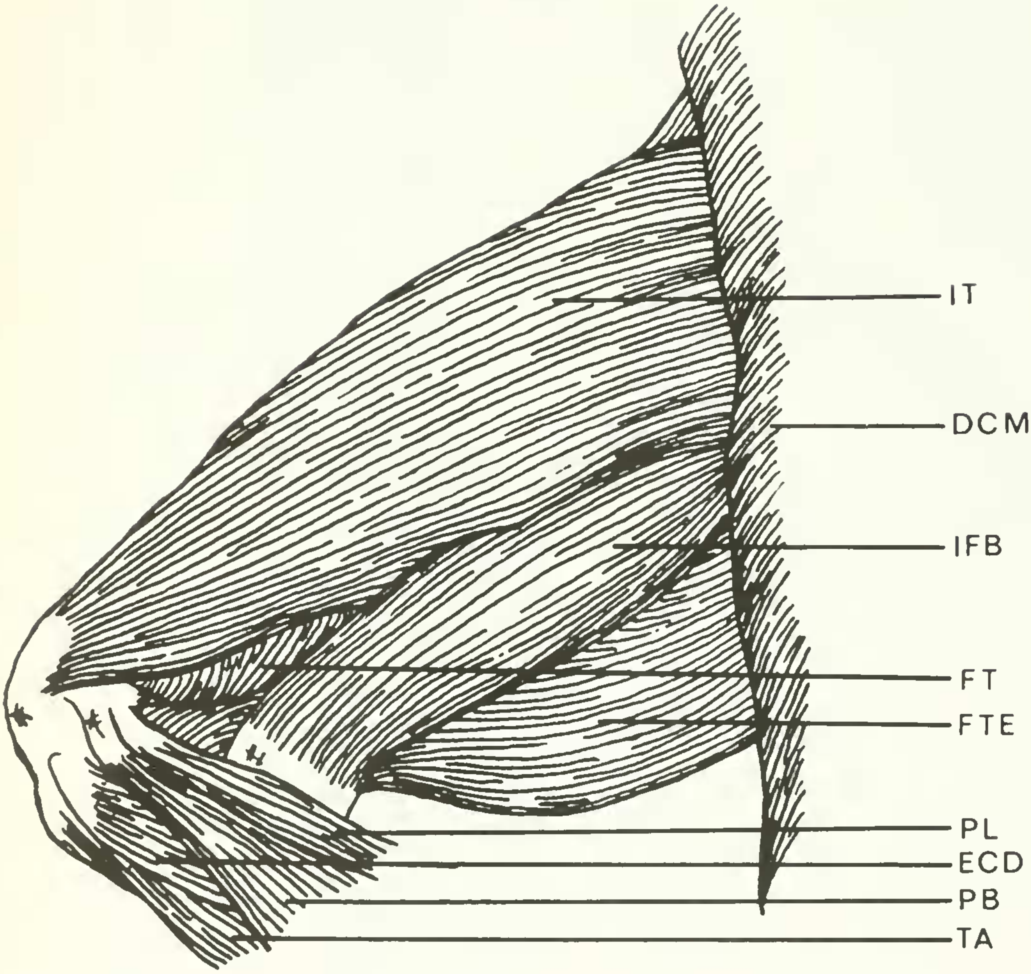

Fig. 6. Dorsal view of superficial musculature of leg.

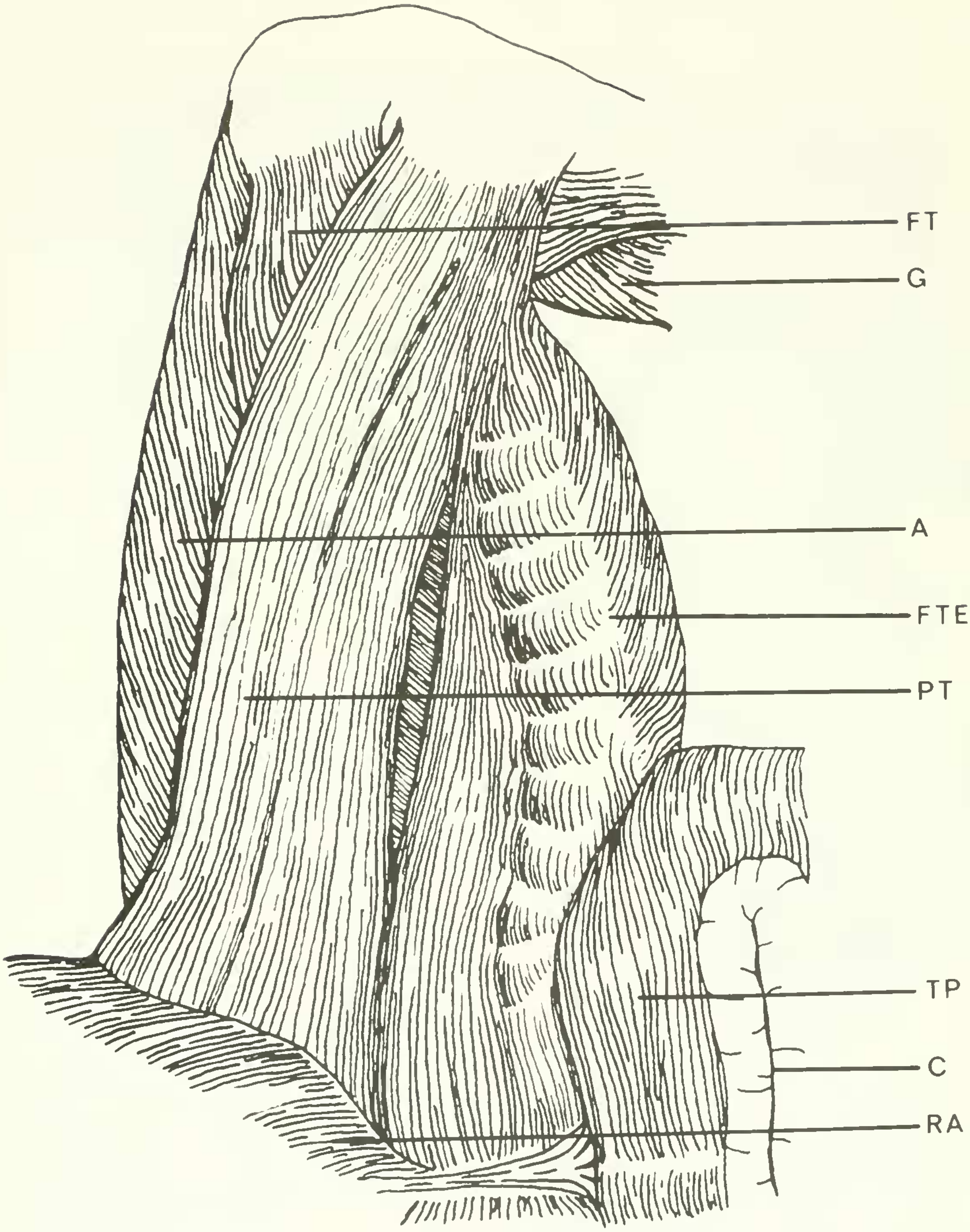

Fig. 7. Ventral view of superficial musculature of leg.

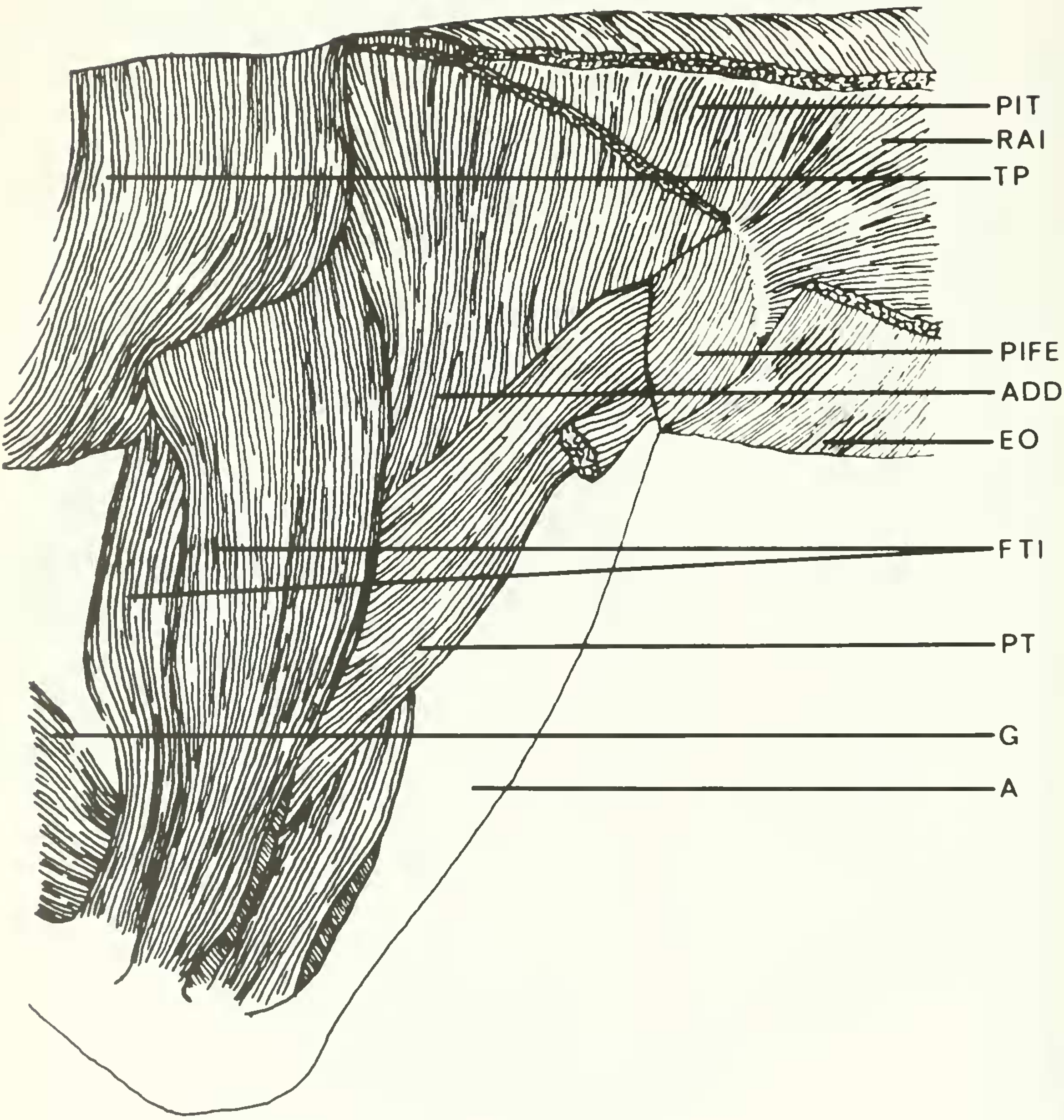

Fig. 8. Ventral view of leg, pubo-ischio-femoralis and flexor tibialis externus removed.

some differences. The intermandibularis anterior and posterior are not separated by fascia as in *Sauromalus*, but they differ from *Sceloporus* in having a definite superficial slip of the anterior. Only two slips of the depressor mandibularis are present in some species of *Crotaphytus*, but three are present in the other species, as in *Sceloporus*. More important are the folded nature of the episternohyoid muscle and the simple nature of the subscapular ligament. The nature of the flexor tibialis externus is not known.

Etheridge (1964) considers *Phrynosoma* to be very closely related to the sceloporine lizards. It differs, according to Camp (1923), by having a very well-developed intermandibularis anterior superficialis. According to the Sanders (1874) the body musculature differs by the absence of the trapezius, an extremely narrow latissimus dorsi and a flexor tibialis externus which crosses the knee independent of the pubo-ischio-tibialis.

Jenkins and Tanner (1968) consider that the myological peculiarities of *Phrynosoma* consist of "The divided nature of the M. sternohyoideus, M. subscapularis II, and M. episternocleidomastoideus, and the reduced condition of the M. serratus, M. trapezius, and M. obliquus abdomniis externus, and the expanded nature of the M. branchiohyoideus . . . " . Therefore, the body musculature is decidedly different.

It has been shown that there are discernible differences between the species of *Sceloporus*. Little pattern can be seen in the differences and one cannot be projected until further work is done.

Even between the closely related *clarki* and *magister* differences can be seen. *Magister* possesses a constrictor colli which is merged with the intermandibularis posterior; the episternohyoideus profundus is not present; and the iliocostalis is much larger than that found in *clarki*.

CONCLUSIONS

1. *Sceloporus* is not closely related to the ground-dwelling *Sauromalus*, *Ctenosaura* and *Dipsosaurus*.

2. *Crotaphytus* is more closely allied to *Sceloporus* than to the ground-dwelling iguanines.

3. The musculature of *Phrynosoma* is aberrant in several respects, while other aspects indicate that its relationship is not as close to *Sceloporus* as is that of *Crotaphytus*.

4. The high degree of development of the subscapular ligament in all species of *Sceloporus* and its associated development in *Iguana*, an arboreal lizard, would indicate the possibility of the basic stock of *Sceloporus* being arboreal. This is born by the nature of the flexor tibialis externus.

5. The small differences in myology between the species of *Sceloporus* would indicate the presence of a rapidly evolving group with, as yet, little morphological variation.

6. Differences in the myology of reptiles can and do occur at the species group and genus group levels.

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